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ARTICLE
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Using passive acoustic monitoring to estimate northern spotted owl landscape use and pair occupancy

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Abstract

Managing forests for biodiversity conservation while maintaining economic output is a major challenge globally and requires accurate and timely monitoring of imperiled species. In the Pacific Northwest, USA, forest management is heavily influenced by the status of northern spotted owls (*Strix occidentalis caurina*), which have been in continued population decline for the past four decades. The monitoring program for northern spotted owls is transitioning from mark–resight surveys to a passive acoustic framework, requiring development of alternative analysis approaches. To maintain relevance for conservation and management, these analyses must accurately track underlying population changes, identify responses to disturbance, and estimate occupancy of owl pairs. We randomly selected and surveyed 5-km^2 hexagons for 6 weeks using passive acoustic monitoring in the Olympic Peninsula of Washington and the Oregon Coast Range during the 2018 spotted owl breeding season. We used a convolutional neural network to identify spotted owl calls, followed by logistic regression to determine the sex of vocalizing owls to assign pair status. We implemented multistate occupancy models to estimate probabilities of detection, species-level landscape use, and pair occupancy of spotted owls. We also quantified detections of barred owls (*Strix varia*), a congeneric competitor and important driver of spotted owl population declines. The overall rate of hexagon use by spotted owls was estimated at 0.21 (SD 0.04) after adjusting for imperfect detection, and pair occupancy was 0.07 (SD 0.02). The probability of detecting a pair (i.e., both female and male) during a weekly occasion was relatively low (0.03, SD 0.01), indicating that true pair occupancy was between 1.3 and 4.1 times greater than the proportion of hexagons with observed pair detections. Barred owls were ubiquitous, with a naïve occupancy rate of 0.97. The intensity of calling by barred owls had a weak, negative effect on the probability of spotted owls being paired when present but had little measurable effect on their detectability. This work establishes a framework that may be effective for spotted owl population monitoring and illustrates that

pairs have very low detection probability, which—combined with increasingly low numbers of spotted owl pairs—is an important consideration for conservation and management.

KEYWORDS
barred owl, bioacoustics, detection probability, occupancy, passive acoustic monitoring, spotted owl

INTRODUCTION

Managing forests for the dual objectives of biodiversity conversation and timber harvest for economic output and resource provisioning is a key challenge around the world. In the United States, the Endangered Species Act (ESA) requires designating critical habitat for imperiled species and provides mechanisms to limit adverse effects resulting from management actions that alter critical habitat on both public and private land. In the Pacific Northwest, USA—one of the largest timber-producing regions in the world—forest management is directly influenced by the status of the ESA-listed northern spotted owl (*Strix occidentalis caurina*, hereafter spotted owl), an iconic species and old-forest obligate. In 1990, due to precipitous population declines related to rapid loss of old-growth forests, the spotted owl was listed as "Threatened" and, due to continued population declines, now warrants uplisting to "Endangered" status (USFWS, 2020). This eventually resulted in the implementation of the Northwest Forest Plan, a broadscale ecosystem management plan that attempted to balance timber extraction with biodiversity conservation of federally managed forests (Thomas et al., 2006). Monitoring of spotted owl habitat and populations is mandated by this Plan and by the species recovery plan to assess population trajectories and inform adaptive management practices (USFWS, 2011). Additionally, survey and consultation mitigation measures are required in areas with proposed timber harvest within the historical range of the spotted owl, with the aim of preventing harm to territorial spotted owls and their habitat and, if necessary, modifying timber harvest plans in areas used by owls. Spotted owl territories are prioritized for protection based on evidence of reproductive activity—specifically, the presence of pairs or resident single spotted owls (USFWS, 2011). Misclassifying the reproductive or occupancy status of spotted owls can thus result in the removal of habitat within occupied territories, to the detriment of the species. Therefore, in addition to long-term monitoring of spotted owls for species recovery planning, the ability to detect spotted owls when present and estimate pair occupancy is critical to maintain the balance between protecting habitat and allowing timber harvest that supports local economies.

The rate of spotted owl habitat loss on federal lands has been slowed due to forest protections under the 1994 Northwest Forest Plan; however, spotted owl populations continue to decline (Franklin et al., 2021). These persistent population declines are driven primarily by continued loss of old forest due to large wildfires and timber harvest on non-federal lands as well as by competition and displacement by congeneric barred owls (*Strix varia*), a recent newcomer to the Pacific Northwest (Davis et al., 2022; Franklin et al., 2021; Lesmeister et al., 2018). Barred owls have been linked to changes in spotted owl behavior and ecology such as reduced niche space, increased adult dispersal, and decreased survival and reproduction (Jenkins et al., 2021; Jenkins, Lesmeister, Forsman, et al., 2019; Jenkins, Lesmeister, Wiens, et al., 2019; Lesmeister et al., 2018; Rockweit et al., 2022; Wiens et al., 2021). Without management intervention, competition by barred owls in combination with declining habitat conditions is expected to cause extirpation of northern spotted owls from parts of their range in the coming decades (Franklin et al., 2021; Yackulic et al., 2019).

During the first phase of population monitoring under the Northwest Forest Plan Effectiveness Monitoring Program (Lint et al., 1999), trends in spotted owl vital rates were estimated using callback surveys and mark–resight methods for several decades, yielding information on population status and responses to environmental disturbance (e.g., Anthony et al., 2006; Dugger et al., 2016; Forsman et al., 2011; Franklin et al., 2021). When the monitoring program was designed, the most appropriate methods to detect population trends were to estimate demographic rates using callback surveys and by capturing, marking, and resighting individual owls through time (Franklin et al., 1996).

Passive monitoring methods (i.e., no elicited responses or live capture) have advanced considerably in the past several decades and, in combination with new modeling approaches, now enable the collection of occurrence data over large spatial and temporal scales (Tosa et al., 2021). To address the difficulty of locating and identifying detections of species of interest from substantial volumes of data, machine learning methods such as convolutional neural networks are increasingly being applied to ecological

datasets (e.g., Norouzzadeh et al., 2017; Ruff et al., 2019, 2021; Sugai et al., 2019; Tabak et al., 2019). Additionally, the development of occupancy models to analyze detection/nondetection data (MacKenzie et al., 2002, 2018) has greatly increased the value of passive monitoring programs. The combination of bioacoustics, neural networks, and occupancy models is a promising approach for monitoring threatened species (Campos-Cerqueira & Aide, 2016) and forest raptors in particular (Duchac et al., 2020, 2021; Maegawa et al., 2021; Shonfield et al., 2018). A new framework using habitat modeling and detection/nondetection data of unmarked owls from bioacoustics is the basis for the second phase of spotted owl monitoring (Davis et al., 2022; Glenn et al., 2017; Lesmeister & Jenkins, 2022; Lint et al., 1999).

Passive acoustic monitoring is effective for detecting the presence of northern spotted owls and barred owls (Duchac et al., 2020) as well as the closely related California spotted owl subspecies (*S. o. occidentalis*) (e.g., Wood, Popescu, et al., 2019, Wood, Schmidt, et al., 2019). Further, methods have been developed to greatly advance the identification and classification of spotted owl calls in acoustic recordings with minimal human effort (Ruff et al., 2019, 2021). Passive acoustic monitoring can also detect declines in spotted owl populations, but the estimated magnitude of decline can be biased low, especially if spotted owls are detected far from their territory centers (Lesmeister et al., 2021). Underestimating population declines is a particular concern for threatened species at low densities, when timely detection of even small population changes is necessary to trigger conservation actions (Conner et al., 2016; Fuller et al., 2022; Lesmeister et al., 2021). Because spotted owls are territorial, a promising way to reduce bias in these estimates is to classify detections as either pairs or nonpairs, which could include transient spotted owls or resident owls conducting wide-ranging movements. For example, Olson et al. (2005) found that occupancy estimates based on detections of paired owls more accurately reflected population dynamics compared with models that included detection/nondetection of any owl.

In addition to range-wide population monitoring, passive acoustic methods are increasingly being used for pre-timber harvest surveys in the Pacific Northwest to ensure that management actions are not undertaken in areas occupied by territorial spotted owls. The ability to estimate the probability of pair occupancy will thus also lead to enhanced utility of passive acoustic pre-project surveys for consultation and management actions as well as for population monitoring. In both cases, occupancy modeling will be an essential tool to estimate the presence of owls and owl pairs on the landscape while accounting for imperfect detection.

The relationship between occupancy and abundance has been an area of interest with regard to appropriate sampling design for highly mobile and rare species (e.g., Fuller et al., 2022; Steenweg et al., 2018; Tempel & Gutiérrez, 2013). The interpretation of occupancy models often assumes closure of occupancy states within a season (MacKenzie et al., 2018), but if individuals move among sampling units, then the results can be interpreted more generally as landscape use rather than occupancy when these detections result in turnover of occupancy status between replicate surveys. The conflation of landscape use with occupancy can lead to underestimating changes in population trends, highlighting the need to correctly classify detections as representative of site occupancy or landscape use (e.g., Berigan et al., 2019; Conner et al., 2016; Lesmeister et al., 2021). Spotted owls are territorial with pairs using a highly restricted area during the breeding season, especially females (Forsman et al., 1984). Detections of pairs within a short window during a breeding season can therefore meet the closure assumption for occupancy models if the spatial extent of sample units is appropriately defined (for example, at least as large as the area used during the breeding season). In contrast, movements by nonpaired owls—or by paired males making movements outside their core areas—may be more appropriately interpreted as landscape use, given the higher likelihood of these individuals being detected at multiple sample units within a short time window and thus violating the assumption of closure necessary for interpretation of occupancy (Steenweg et al., 2018). Here, we distinguish between detections of female and male spotted owls in close proximity (hereafter pair occupancy) and detections of spotted owls not identified as a potential pair, representing species-level landscape use.

Identifying potential spotted owl pairs from passive acoustic recordings requires extracting biological information beyond species-level detection/nondetection data. Others have demonstrated identifying sex-specific calling and reproductive status from acoustic detections for various species (Teixeira et al., 2019), including birds of prey (e.g., Dale et al., 2022; Maegawa et al., 2021; Wood et al., 2021). Like many other species of birds, owls are distinguishable by sex based on differences in vocal pitch, call type, duration, and other characteristics of calling behavior, which can help identify potential pairs in acoustic detections (Dale et al., 2022; Forsman et al., 1984; Ganey, 1990; Odom & Mennill, 2010; Volodin et al., 2015).

Here, we fit multistate occupancy models to passive acoustic monitoring data to estimate probabilities of detection, landscape use, and pair occupancy for spotted owls. We demonstrate a data processing workflow for locating and identifying calls of spotted owls and barred owls, determining the sex of the vocalizing spotted owls,

and creating multistate detection histories. This process utilizes a trained convolutional neural network developed by the Pacific Northwest Bioacoustics Lab (PNW-Cnet; Ruff et al., 2021) and a predictive model to distinguish between calls of female and male spotted owls based on variation in vocal pitch (Dale et al., 2022). Further, we incorporate a covariate of calling intensity by barred owls to investigate their effects on detectability, landscape use, and pair occupancy of spotted owls. Our objective was to establish an analytical framework for spotted owl population monitoring that can be used to assess population trends, conservation needs, habitat protections, and effects of landscape disturbance.

METHODS

Study area

We conducted passive acoustic monitoring on the Olympic Peninsula in Washington (OLY; approximately 3750 km^2) and in the Oregon Coast Range (COA; approximately 3576 km^2) in the Pacific Northwest, USA (Figure 1). These study areas were locations used in the Northern Spotted Owl Effectiveness Monitoring Program for the Northwest Forest Plan (Dugger et al., 2016; Franklin et al., 2021; Lint et al., 1999). Sample units were 5-km^2 hexagons chosen randomly from a grid overlaid across the spotted owl's geographic range at approximately 20% density within each study area, resulting in 88 surveyed hexagons in OLY and 119 in COA (Figure 1) (Lesmeister et al., 2019, 2022). Hexagons selected for monitoring contained ≥50% forest-capable land—defined as areas capable of developing forest cover (Davis et al., 2015)—and ≥25% federally managed lands, primarily administered by the U.S. Forest Service, Bureau of Land Management, and the National Park Service. Forested areas in both study areas were primarily dominated by Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*) cover types. Monitored stations ranged in elevation from 42 to 1545 m in OLY and from 68 to 753 m in COA.

Data collection and processing

We used a hierarchical sampling design based on the grid of 5-km^2 hexagons, which is larger than most reported spotted owl breeding core areas and is approximately the mean home range size for barred owls reported in the Pacific Northwest (Wiens et al., 2014). Each 5-km^2 hexagon contained five randomly located survey stations spaced ≥500 m apart. At each station, we attached an autonomous recording unit (ARU) (Song Meter SM4, Wildlife Acoustics; Maynard, MA) to a tree (10–20 cm diameter), 2 m aboveground (Lesmeister et al., 2019). The ARUs were deployed for 6–8 weeks during the spotted owl breeding season (March–September 2018) and were programmed to record continuously during crepuscular periods (1 h before to 3 h after sunset; 2 h before to 2 h after sunrise), when spotted owls are most vocally active (Duchac, 2019).

We converted audio recordings to spectrogram images and processed them using the multiclass PNW-Cnet developed by Ruff et al. (2021), which identified 12 bird calls and songs and vocalizations from 2 mammal species of interest in the Pacific Northwest. These calls included territorial calls of spotted owls (4-note hoots) and barred owls (8-note hoots) as well as barred owl inspection calls (Odom & Mennill, 2010). We split each hour of recording into 300 nonoverlapping 12-s clips and converted each clip to a spectrogram by applying Fourier transformations to represent sound energy as a function of both frequency and time (Figure 2). The spectrograms were then processed through the PNW-Cnet for predictions and assigned a vector of class scores, representing the confidence that a given 12-s clip contained a signal matching each target class. Clips with a class score of ≥25% for spotted owls or ≥95% for barred owls were considered potential detections and were then manually validated. We used a conservative threshold to maximize recall of spotted owl calls and reviewed all potential detections to reduce the possibility of including false-positive detections (e.g., domestic dog barking, calls by other owl species). Although other spotted owl call types were not included as PNW-Cnet target classes, when we encountered these calls during the validation process, we included them as detections. These included series location calls, barks, duets, and caterwauling, but not juvenile begging calls or contact whistles, which are more difficult to distinguish between the *Strix* species.

Callback surveys for spotted owls and barred owls for other studies (Franklin et al., 2021; Wiens et al., 2021) also occurred during our surveys, so we removed potential detections that were human callback surveys and spotted owls responding to those surveys. We removed all potential spotted owl detections that occurred on the same night as documented spotted owl callback surveys in hexagons that overlapped reported survey areas, which also ensured that we only considered natural (i.e., not elicited) calling behavior. We also removed calls that were clearly not real owls (e.g., "hoot flute" devices) regardless of whether they matched recorded survey times. For barred owls, to remove potential contamination of our data by detections of surveyors, we removed detections that occurred on the same night as documented barred owl

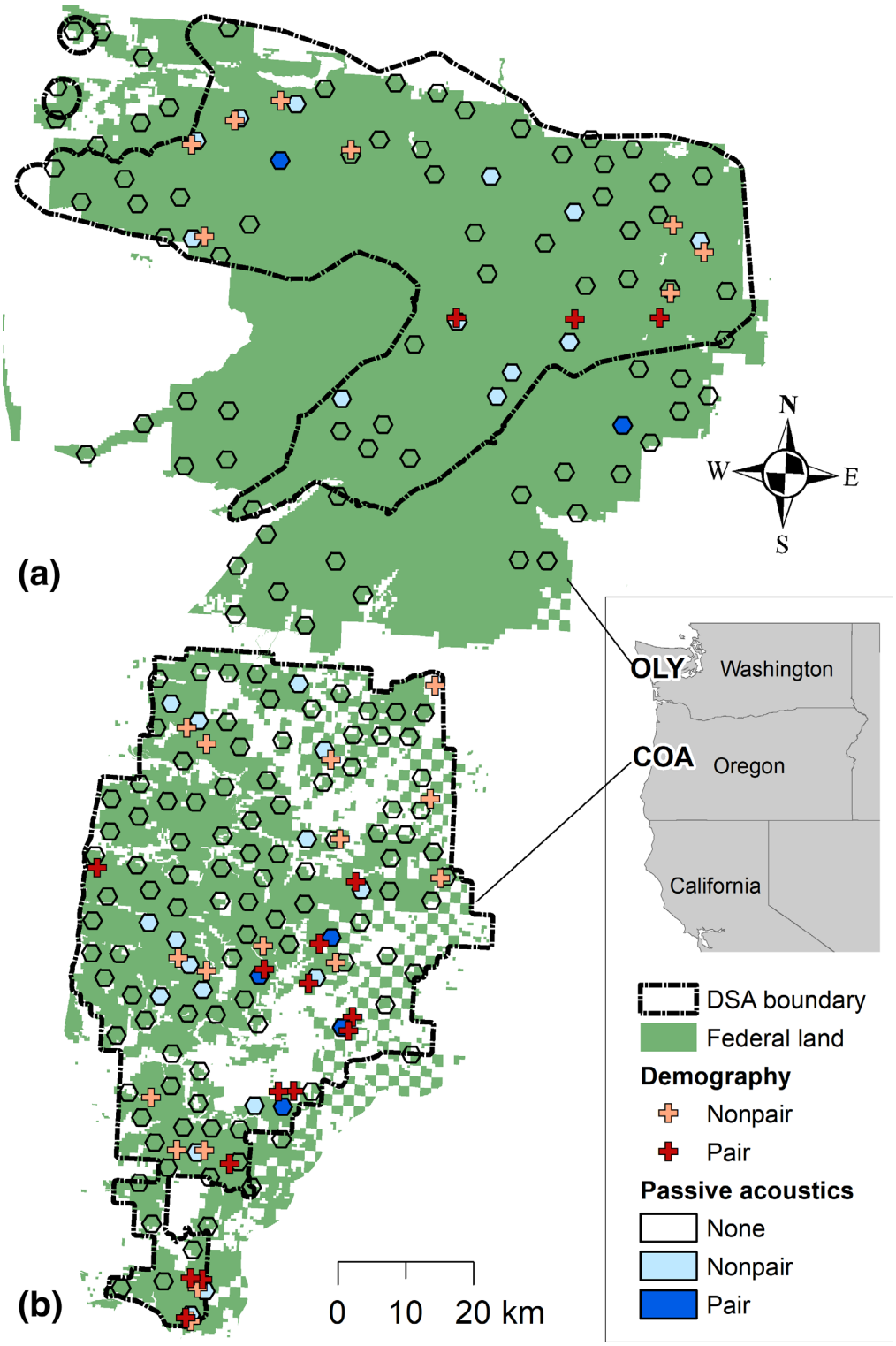

FIGURE 1 Study areas for passive acoustic monitoring of northern spotted owls in 2018 within and surrounding the (a) Olympic Peninsula (OLY) and (b) Oregon Coast Range (COA) demographic study areas (DSAs) in the Pacific Northwest, USA. All monitoring occurred on federal land. Each 5-km^2 hexagon ($n = 119$ COA, 88 OLY) contained ≤5 autonomous recording unit stations randomly placed ≥500 m apart. Hexagons are shaded according to the observed state used in multistate occupancy models, based on detections of paired or nonpaired spotted owls using passive acoustic monitoring. Also shown are independent locations of paired and nonpaired spotted owl activity centers from demography surveys in 2018 (Franklin et al., 2021).

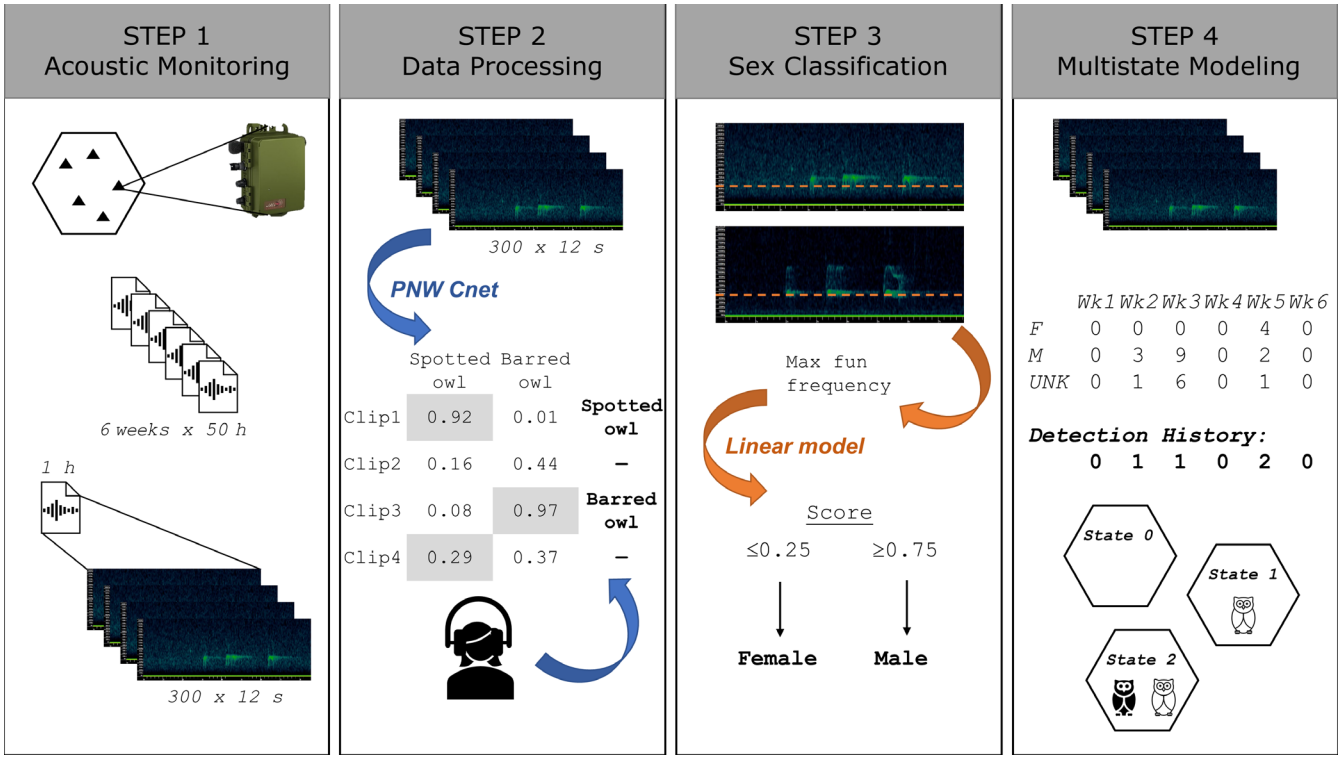

FIGURE 2 Workflow for collecting, processing, and analyzing data from passive acoustic monitoring for northern spotted owls in the Oregon Coast Range and Olympic Peninsula in 2018. In Step 1, data were collected using autonomous recording units (ARUs) placed ≥500 m apart in 5-km^2 hexagons, with each ARU recording 50 h/week for 6 weeks. Each 1-h audio segment was divided into 300 nonoverlapping 12-s clips, which were each converted to a spectrogram image displaying sound energy as a function of frequency and time. In Step 2, spectrograms were processed through a convolutional neural network (PNW-Cnet; Ruff et al., 2021), which produced confidence scores (0–1) for whether each clip contained a signal matching a target class, including calls by northern spotted owls and barred owls. Clips with class scores ≥0.25 for spotted owls and ≥0.95 for barred owls (shaded cells) were manually reviewed to determine the correct class in each clip (bold). In Step 3, spectrograms with confirmed spotted owl calls were analyzed to determine the maximum fundamental frequency of the middle two notes of a 4-note call, and these values were used to make out-of-sample predictions from a linear model (Dale et al., 2022) to determine the sex of the vocalizing owl (model scores ≤0.25 were females, ≥0.75 were males). Step 4 consisted of constructing weekly multistate detection histories based on whether ARUs in each hexagon detected no spotted owls (state 0), detected spotted owls but no confirmed females (state 1), or detected both female and male spotted owls (state 2). These detection histories were then used for multistate occupancy modeling as described in the text.

callback surveys or removal activities (Wiens et al., 2020, 2021) in hexagons that either matched or were adjacent to hexagons with reported survey activity, due to the greater distance that these broadcasted recordings can travel, following methods by Duchac et al. (2020). We did not remove barred owl calls that co-occurred with documented spotted owl surveys because we considered it likely that barred owl calling could still have an effect on spotted owls regardless of whether the calling was in response to surveyors.

We created weekly multistate detection histories for each hexagon, representing whether any 12-s clips were confirmed as spotted owls during each survey week period at each of the five stations within the hexagon. For barred owls, we summed the number of detections during each week—including 8-note hoots, inspection calls, and other call types—at each station.

State assignment

Vocal pitch and other acoustic metrics can be used to differentiate calls by females and males of various bird species (Volodin et al., 2015). Territorial calls of female spotted owls are higher in frequency and shorter in duration than territorial calls by males (Dale et al., 2022; Forsman et al., 1984). We used the package warbleR (Araya-Salas & Smith-Vidaurre, 2017) in Program R version 3.6.3 (R Development Core Team, 2020) to extract frequency metrics from the audio clips, focusing on the middle two notes of the 4-note hoot or series location call. We then made out-of-sample predictions using a previously developed linear regression model that differentiated female from male spotted owl calls based on maximum fundamental frequency of these notes

(Dale et al., 2022). We used the model score, or probability that a given clip was male, to assign predictions of female (≤0.25), male (≥0.75), or undetermined sex (0.26–0.74) to calls in each clip.

A random subset (20%) of these clips was also examined by an expert reviewer to determine the sex of the vocalizing owl. We measured model performance by comparing model predictions and expert reviewer determinations with calculations of precision, recall, and F1 scores (Appendix S1). Where model predictions differed from expert review, and for clips with model predictions that were inconclusive or for which frequency metrics could not be extracted due to low quality, we reviewed the clips and attempted to make a judgment on the correct sex classification. For calls that were not 4-note hoots or series location calls, we did not attempt to determine the sex of the vocalizing owl, with the exception of female barks, which are a diagnostic call type for female spotted owls (Forsman et al., 1984).

A preliminary review of the 2018 data revealed that in all hexagons where female spotted owls were detected, we also detected male spotted owls either at the same station in the same week, in the same week at a different station, or in a different week at the same station. Additionally, females are known to call less frequently than males (Ganey, 1990; Reid et al., 1999) and pair activity is restricted to a small core area (Forsman et al., 1984), suggesting that co-occurrence of female and male calls in the same 5-km^2 hexagon could be interpreted as potential pair behavior. Thus, we considered hexagons with female and male detections to have the highest occupancy state of a potential pair. Hexagons with detections of spotted owls, but no evidence of pair behavior (i.e., no females detected), were treated as the lower state, contributing only to species-level landscape use by spotted owls. We assumed the true states for each hexagon were occupied by a spotted owl pair (state 2), used by spotted owls but not by a pair (state 1), or not used by owls (state 0). Based on these definitions and the sex of the spotted owls in each audio clip, we recorded observed states for each station-week period as follows:

0 = spotted owls not detected [true state = 0, 1, or 2];
1 = spotted owls detected, but no female calls (i.e., only calls of males or owls of undetermined sex, or call types that are not diagnostic of sex) [true state = 1 or 2];
2 = at least one female call detected [true state = 2].

For our models, we used a conditional probability parameterization to correctly classify the true state when the species was undetected and when the species was detected but we failed to detect females when they were present (Nichols et al., 2007).

To further support our assumption that calls of females in a hexagon (again, all also had males detected) represented a potential pair, we compared our detections with an independent dataset of spotted owl activity center locations from demographic surveys (Franklin et al., 2021). Where we detected potential pairs, female calls were never detected in more than one surveyed hexagon within a 10-km radius, although males or nondiagnostic calls were sometimes detected in nearby hexagons (Figure 1). In COA, all four hexagons where we recorded potential pairs had at least one confirmed pair activity center within 2 km (Figure 1). In OLY, neither hexagon where we recorded a potential pair had a confirmed pair within 20 km, but these hexagons were located either outside the demographic study area or where low survey effort occurred (Figure 1). Therefore, we were confident that females were never detected in more than one hexagon, and if we detected individual owls at multiple hexagons—representing landscape use—these would likely have been males and only classified as part of a pair in hexagons where we also detected females during the 6-week survey. We thus assumed closure for pairs such that state 2 represented pair occupancy, while nonpair detections contributed only to species-level landscape use (state 1).

Statistical analyses

We fitted multistate occupancy models in a Bayesian framework to estimate landscape use and pair occupancy of spotted owls at the hexagon scale (i.e., hexagons were treated as our sample units). We assumed that repeated station-level surveys within a hexagon were independent Bernoulli trials, and we considered individual stations and survey weeks to be replicate surveys (5 stations × 8 weeks = 40 survey occasions). This structure was chosen in order to incorporate conditions that influence detection at the level of individual ARU stations to ensure that their effects were accurately evaluated (e.g., Duarte & Peterson, 2021).

Using multistate occupancy models (MacKenzie et al., 2018; Nichols et al., 2007), we estimated the probability of use by spotted owls regardless of pair state (ψ) and the probability that spotted owls were paired given that they were using a hexagon (R). Additionally, we estimated the probability of detecting spotted owls in a station–week period, given that the hexagon had true state 1 (p_1) or state 2 (p_2), as well as the conditional probability of finding evidence of pairing (δ) to account for instances when we detected the species but failed to detect females when they were present. Following MacKenzie et al. (2018) and Nichols et al. (2007), for each survey k, the probabilities of observing each state (columns: 0, 1, 2) given the true state (rows: 0, 1, 2) were estimated as follows:

$$p_k = \begin{Bmatrix} 1 & 0 & 0 \\ 1-p_{1,k} & p_{1,k} & 0 \\ 1-p_{2,k} & p_{2,k}\times(1-\delta_k) & p_{2,k}\times\delta_k \end{Bmatrix}.$$

To account for relationships between environmental conditions and the presence and detectability of spotted owls, we used a logit link to incorporate explanatory variables on several parameters in our model. We were particularly interested in testing whether ψ and R for spotted owls were affected by the amount of barred owl calling nearby. We also allowed ψ and R to vary between the two study areas (COA or OLY) and in relation to the suitability of forest for nesting and roosting within a combined 500-m buffer around all stations in a hexagon (Table 1; Appendix S2: Figure S1). Probabilities p_1 and p_2 were each modeled as a function of several time-varying variables. We suspected that detectability of spotted owls may be affected by background noise (Duchac et al., 2020), survey effort, period of the season during which each ARU was deployed (before or after 12 June), and the amount of barred owl calling nearby. We also included a covariate measuring the suitability of forest for nesting and roosting within 200 m of each ARU to account for the process of owls being available for detection (Table 1; Appendix S2: Figure S1). Because overall detection probability has been found to vary between sites used by single or paired spotted owls (Duchac et al., 2020), we included an intercept adjustment γ_1 on p_2 to allow for differing parameter estimates based on state. However, slope coefficients were shared between covariates on p_1 and p_2 because we did not expect variables to affect detection probability of paired or nonpaired owls differently (i.e., an additive model). The probability δ was not modeled with any explanatory variables.

TABLE 1 Descriptions and summary statistics for explanatory variables used in multistate models used to estimate use (ψ), conditional occupancy by pairs (R), and detection probability for nonpaired (p_1) and paired (p_2) northern spotted owls in the Oregon Coast Range (COA) and Olympic Peninsula (OLY) using passive acoustic monitoring in 2018.

Variable	Unit	Description	Model parameters	Summary[a]
Site level				
STUDY_AREA	NA	Indicator for OLY or COA study area	ψ, R	88; 119
NR_SUIT_{500m}	NA	Mean of nesting–roosting (NR) forest suitability index (Davis et al., 2022) at 30-m^2 cells within 500-m buffers of each station, unionized by hexagon (continuous)	ψ, R	0.30 (0.10); 0.10 to 0.57
BO_{total}	No. calls	Total no. barred owl (BO) detections at all stations within each hexagon (continuous)	ψ, R	774 (809); 0 to 5269
Survey level				
NOISE	dBFS	Mean weekly background noise level in decibels below full scale (dBFS) per station (continuous)	p_1, p_2	−103.0 (8.6); −120.6 to −58.1
EFFORT	Min	Total no. recording minutes per station per week (continuous)	p_1, p_2	3040 (766); 60 to 3360
SEASON	NA	Indicator for when each survey occasion occurred: early (3 March–11 June) or late season (12 June–11 September)	p_1, p_2	4672; 3400
BO_{weekly}	No. calls	Total no. BO detections per station per week (continuous)	p_1, p_2	24 (52); 0 to 905
$NR\_SUIT\_STN_{200m}$	NA	Mean of NR forest suitability index (Davis et al., 2022) at 30-m^2 cells within 200-m buffers of each station (continuous)	p_1, p_2	0.31 (0.14); 0.0 to 0.62

Note: Values for the study area are given as the number of hexagons in OLY (0) and COA (1) and values for season are given as the number of survey occasions during early (0) and late (1) seasons. All other values are means with SD in parentheses and ranges.

[a]All continuous variables were subsequently standardized to have mean = 0 and SD = 1.

The equations for estimating parameters for each hexagon i at station j in survey k were as follows:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 \times \text{NR\_SUIT\_500}_i + \beta_2 \times \text{STUDY\_AREA}_i + \beta_3 \times \text{BOtotal}_i,$$

$$\text{logit}(R_i) = \alpha_0 + \alpha_1 \times \text{NR\_SUIT\_500}_i + \alpha_2 \times \text{STUDY\_AREA}_i + \alpha_3 \times \text{BOtotal}_i,$$

$$\text{logit}\left(p_{1(j,k)}\right) = \gamma_0 + \gamma_2 \times \text{NOISE}_{j,k} + \gamma_3 \times \text{EFFORT}_{j,k} + \gamma_4 \times \text{SEASON}_{j,k} + \gamma_5 \times \text{BOweekly}_{j,k} + \gamma_6 \times \text{NR\_SUIT\_STN\_200}_j,$$

$$\text{logit}\left(p_{2(j,k)}\right) = \gamma_0 + \gamma_1 + \gamma_2 \times \text{NOISE}_{j,k} + \gamma_3 \times \text{EFFORT}_{j,k} + \gamma_4 \times \text{SEASON}_{j,k} + \gamma_5 \times \text{BOweekly}_{j,k} + \gamma_6 \times \text{NR\_SUIT\_STN\_200}_j,$$

$$\text{logit}(\delta) = \iota_0.$$

From this model structure, we derived the probabilities that a hexagon was used and occupied with a pair $\psi_{\text{pair}} = \psi \times R$, used but not occupied by a pair $\psi_{\text{nonpair}} = \psi \times (1-R)$, or not used $\psi_{\text{unused}} = 1 - \psi$. The probability we detected the species when there was a pair present and correctly classified it as a pair was calculated as $p_{\text{pair}} = p_2 \times \delta$. Using Bayes' theorem, we also calculated the conditional probability that if we detected any spotted owls at a station, the true occupancy state of owls in the hexagon was used and occupied by a pair:

$$\begin{aligned}
&\Pr(\text{site occuped by pair} \mid \text{any owl detected}) \\
&= \frac{\Pr(\text{any owl detected} \mid \text{site occupied by pair}) \times \Pr(\text{site occupied by pair})}{\Pr(\text{any owl detected})} \\
&= \frac{p_2 \times \psi_{\text{pair}}}{(p_2 \times \psi_{\text{pair}}) + (p_1 \times \psi_{\text{nonpair}})}.
\end{aligned}$$

Finally, we calculated the probability that a hexagon was used by owls given we did not detect owls there (ψ_{cond}) following MacKenzie et al. (2018):

$$\psi_{\text{cond}} = \frac{\psi \times (1-p_1)^{jk}}{1 - \psi \times [1-(1-p_1)^{jk}]},$$

where jk is the number of unique surveys (weeks × ARUs). For simplicity, we used the detection probability for stations with nonpaired owls (p_1). From this, we estimated the proportion of hexagons used by spotted owls in our sample area ($\widehat{\psi}$) as:

$$\widehat{\psi} = \frac{s_{\text{D}} + (s - s_{\text{D}}) \times \psi_{\text{cond}}}{s},$$

where s is the total number of hexagons surveyed and s_{D} is the number of hexagons with detections (MacKenzie et al., 2018).

Explanatory variables

We described variables by their mean, standard deviation, and range of values (Table 1). We tested for pairwise correlations between covariates using the corrplot package (Wei & Simko, 2017) in Program R and did not use covariates in the same model if the correlation coefficients were high (Spearman $\rho > |0.6|$) (Appendix S2: Figures S2 and S3). We standardized and scaled all continuous covariates to have mean = 0 and SD = 1.

Study area

Surveys were conducted in the OLY and COA study areas, which have different densities of spotted owls, breeding success, and rates of barred owl occupancy (Franklin et al., 2021; Yackulic et al., 2019). Therefore, we used a site covariate indicating whether each hexagon was located in the OLY or COA study area.

Noise

We estimated background noise in all audio recordings using the Sound Pressure Level analysis tool in Kaleidoscope Pro software (Wildlife Acoustics; Maynard, MA). We structured the noise covariate as the mean weekly decibels below full scale (dBFS) across all frequency bands from approximately 250 to 1000 Hz at each ARU station. We expected background noise to have a negative effect on detection probability for spotted owls, as has been found previously (Duchac et al., 2020).

Survey effort

All ARUs were scheduled to record 8 h/day, but actual recording time varied at the beginning and end of surveys due to initial deployment time and ARU or battery failure. We calculated the total number of recording minutes by each ARU per week as a measure of survey effort. Several ARUs ($n = 8$) recorded past the intended schedule of 3360 min/week, but we truncated effort for these at 3360 min as we expected diminishing returns on

detection probability outside the crepuscular period (Duchac, 2019).

Early or late season

Because deployments of ARUs were staggered throughout the March–July period, we attempted to account for the day of the season on which recording began at each station for each weekly period. Distribution of these dates was bimodal due to phased deployments in order to move equipment between stations (Appendix S2: Figure S4). This was not a concern based on previous findings that detectability of spotted owls did not differ throughout the breeding season in targeted sampling (Duchac et al., 2020); however, we allowed for the possibility that detection probability differed by occupancy states in random broadscale sampling. We converted the date of season to a factor covariate, indicating whether each station–week period occurred during the early or late season. We used a cutoff of 12 June to differentiate between the two phases, based on the date when the fewest number of hexagons would have their recordings split between phases.

Barred owls

We created a covariate of barred owl calling by summing the number of clips containing barred owl detections by station and week for each hexagon. Because barred owls were ubiquitous in both study areas, we considered the amount of barred owl calling—rather than barred owl presence—that may have affected spotted owl landscape use, pair occupancy, and detection.

Nesting–roosting forest suitability

We used an index of nesting–roosting (NR) forest suitability to incorporate a known relationship between spotted owl occurrence and availability of forest types required for breeding (Davis et al., 2022). This covariate was represented by an index (0–1) of how similar a given cell (30 × 30 m) was to other areas with known spotted owl NR sites based on tree species composition and structural factors. For the survey-level covariate on detection probability, we used the mean suitability value in cells within a 200-m buffer of each station to approximate a likely listening distance of the ARUs (Hane et al., 2022; Maegawa et al., 2021; Wood et al., 2021) while minimizing the amount of overlap between station buffers (Appendix S2: Figure S1). For the hexagon-level covariate on occupancy, we used the mean suitability value within a 500-m buffer around each ARU station, unionized to create a single footprint per hexagon (Appendix S2: Figure S1). This buffer size was chosen to represent the coverage of the broader area spotted owls may use within a hexagon, beyond just where they were detected.

Modeling approach

We used multiple lines of evidence to predict landscape use, pair occupancy, and detection probabilities and to make inference on the effects of explanatory variables. To identify the best model for predicting pair occupancy and landscape use, we used the indicator variable approach described by Kuo and Mallick (1998) for Bayesian model selection (Kéry & Royle, 2016). We used a sequential-by-submodel process (Morin et al., 2020), focusing on model structure separately for p_1 and p_2, ψ, and R in that order. We first fitted a fully parameterized submodel for p_1 and p_2 with intercept-only structure on ψ and R. We used this most supported submodel structure for p_1 and p_2 while testing a fully parameterized submodel for ψ and then additionally retained the most supported model for ψ during model selection for R. Following Duarte et al. (2020) and Jiménez et al. (2017), we used spike-and-slab priors to ensure that covariates were not overly prone to omission due to their indicator values always assuming a value of 0 (Mitchell & Beauchamp, 1988). To obtain tuning parameters for the spike-and-slab priors, we initially ran submodels using coefficients with prior probabilities $\text{Normal}(\mu = 0, \tau = 0.368)$ to approximate a uniform distribution on the probability scale. For submodel selection, we then used the coefficient posterior means and standard deviations from these models as tuning parameters for spike-and-slab priors on all covariates, which were also multiplied by indicator variables with prior probabilities $\text{Bernoulli}(\mu = 0.5)$ such that they assumed values of either 0 or 1. We selected the model structure using the combination of indicator variables occurring most often throughout the Markov chain Monte Carlo (MCMC) iterations by retaining the predictors for which the indicator variables in this most frequent combination took the value of 1. After model selection, we fit the best model again without indicator variables using the original diffuse priors and used estimates from this model for inference. We report derived parameter estimates from this model as the mean and standard deviation of the inverse-logit-transformed posterior draws with 95% credible intervals (CI).

Because we were also interested in interpreting covariate relationships on the use and occupancy parameters, we also fitted the fully parameterized model with all predictors on ψ and R regardless of whether they were

retained during submodel selection, but maintained the reduced set of parameters on p as they were not relevant to the ecological process of interest. We interpreted the magnitude and direction of the covariate effects based on marginal plots, parameter estimates, odds ratios, and F-scores—the proportion of the posterior density above or below 0—that is, the probability of an effect being either positive or negative. Odds ratios were calculated as the median of the exponentiated posterior draws. For this model, we tested prior sensitivity using three prior sets: $\text{Normal}(\mu = 0, \tau = 0.368)$, $\text{Normal}(\mu = 0, \tau = 0.5)$, and $\text{Uniform}(\min = -5, \max = 5)$ to ensure that inference was not sensitive to prior specification (Northrup & Gerber, 2018). We plotted parameter estimates to assess pairwise agreement among models with each prior set.

Models were run by calling JAGS (Plummer, 2003) in Program R using the jagsUI package (Kellner, 2019). We ran models with three or more independent MCMC chains each consisting of 50,000 iterations, following burn-in and adaptation phases of 50,000 iterations each. For all models, we visually inspected posterior trace and density plots for evidence of nonconvergence and ensured $\widehat{R}$ values were <1.1 (Brooks & Gelman, 1998).

RESULTS

Data collection and processing

We collected and processed 342,508 h of audio data from 1009 ARUs in 207 hexagons from 7 March to 13 September 2018. ARUs recorded for a mean of 50.7 h/week (SD 12.8 h) for an average of 6.0 weeks (SD 0.9 weeks), in comparison to our intended schedule of 56 h/week for 6 weeks. Survey start dates ranged between 7 March 2018 and 27 July 2018 for logistical reasons and because within-breeding season variation in spotted owl detection probabilities using ARUs has not been observed (Duchac et al., 2020).

After reviewing potential detections identified by the PNW-Cnet and removing recordings of surveyors rather than real owls, we verified 1490 audio clips with calls from spotted owls, of which 85% ($n = 1269$) were 4-note hoots and 15% ($n = 221$) were other call types (e.g., series location calls or barks). Spotted owl calls were recorded in 34 of the 207 hexagons surveyed (16.4%) and at 67 of 1009 ARU stations (6.6%). Of the 34 hexagons with detections, we most commonly observed spotted owls at only one (41%; $n = 14$ hexagons) or two (38%; $n = 13$) ARU stations. Only one hexagon had spotted owl detections at all five ARU stations. The earliest and latest spotted owl detections occurred on 16 March 2018 and 10 September 2018, respectively. Mean latency to first detection among all hexagons was approximately 16 days (SD 12 days, range 0–36 days).

From the same set of recordings, we identified 160,814 clips containing barred owl calls from 200 of the 207 hexagons. Sixty-one percent of these clips ($n = 98{,}394$) were the 8-note territorial hoots, while 19% ($n = 30{,}991$) were "irregular" call types (e.g., ascending hoots, 2- or 3-note hoots, and duets; Odom & Mennill, 2010) and 18% ($n = 28{,}822$) were barred owl inspection calls. The remaining 2% of clips ($n = 2607$) contained multiple call types. In contrast to the hexagons with spotted owl detections, 57% of hexagons ($n = 115$ hexagons) with barred owls had detections at all five ARU stations. Only 4% of hexagons ($n = 9$) with barred owls had detections at only one ARU station. The earliest and latest barred owl detections occurred on 7 March 2018 and 13 September 2018, respectively. Mean latency to first detection for barred owls at the hexagon level was approximately 3 days (SD 6 days, range 0–40 days).

State assignment

We used the linear regression model (Dale et al., 2022) to predict the sex of the vocalizing spotted owls in 814 calls from 25 of the 34 hexagons where spotted owls were detected (Appendix S1). The remaining calls ($n = 724$) were either low-quality recordings from which maximum fundamental frequency could not be extracted or did not include 4-note hoots. Model performance for our test set was high, with F1 scores of 88.9% and 98.2% for females and males, respectively, and overall accuracy of 95.1% (Appendix S1). After making final determinations, we identified 112 female spotted owl calls from 6 hexagons and 540 male calls from 34 hexagons.

Statistical analysis

The most supported model for detection and occupancy probabilities included additive effects of NOISE and EFFORT on detection and an intercept-only structure for δ, ψ, and R (Table 2). After accounting for imperfect detection, we estimated the overall probability of spotted owl use regardless of pair state (ψ) at 0.206 (CI 0.143–0.282) (Table 3), compared with the naïve occupancy rate of 0.164 (i.e., the proportion of hexagons with detections without factoring in detectability). The estimated probability of landscape use by nonpaired owls ($\psi_{\text{nonpair}} = 0.132$, CI 0.078–0.200) (Table 3) was similar to the observed proportion of hexagons with detections but no pair confirmed (0.135). However, the derived occupancy rate by spotted owl pairs ($\psi_{\text{pair}} = 0.074$, CI 0.037–0.119) was estimated to be between 1.3 and 4.1 times

TABLE 2 Top models for each step in sequential-by-submodel selection using latent indicator variables to compare support for explanatory variables associated with occupancy and detection probability of northern spotted owls in the Oregon Coast Range and Olympic Peninsula using data from passive acoustic monitoring in 2018.

Parameter	Covariate structure	Proportion of iterations[a]
Step 1: p(NOISE + EFFORT + SEASON + BO_{weekly} + $NR\_SUIT\_STN_{200m}$) δ(.) ψ(.) R(.)		
p	**p(NOISE + EFFORT)**	**0.610**
	p(NOISE + EFFORT + SEASON)	0.119
	p(NOISE + EFFORT + $NR\_SUIT\_STN_{200m}$)	0.099
	p(NOISE)	0.072
	p(NOISE + EFFORT + BO_{weekly})	0.033
Step 2: p(NOISE + EFFORT) δ(.) ψ(NR_SUIT_{500m} + STUDY_AREA + BO_{total}) R(.)		
ψ	**ψ(.)**	**0.466**
	ψ($NR\_SUIT\__{500m}$)	0.229
	ψ(STUDY_AREA)	0.122
	ψ(BO_{total})	0.066
	ψ(NR_SUIT_{500m} + STUDY_AREA)	0.058
Step 3: p(NOISE + EFFORT) δ(.) ψ(.) R(NR_SUIT_{500m} + STUDY_AREA + BO_{total})		
R	**R(.)**	**0.327**
	R(STUDY_AREA)	0.193
	R(BO_{total})	0.131
	R(NR_SUIT_{500m})	0.121
	R(STUDY_AREA + BO_{total})	0.076

Note: Parameters estimated in the models were probability of landscape use by spotted owls regardless of pair state (ψ), probability that spotted owls were paired given that they were using a hexagon (R), and probability of detection given presence (p). The top five submodels for each step are listed with the proportion of model iterations with that combination of variables. Models in bold represent the submodel structure carried forward to the next step.
[a]Out of 50,000 iterations.

higher than naïve occupancy by pairs (0.029), suggesting that for many spotted owl pairs, the females went undetected.

The probability of detecting any spotted owl at an ARU station during a weekly survey was higher in hexagons with pairs ($p_2 = 0.169$, CI 0.129–0.214) compared with hexagons with only species-level landscape use ($p_1 = 0.037$, CI 0.020–0.062) (Table 3). However, we estimated a low probability of detecting pairs and correctly classifying them as a pair (i.e., detecting a female) in hexagons where they were present ($p_{pair} = 0.032$, CI 0.017–0.054) due to the low calling rates by females. This means that at hexagons with spotted owl pairs, only calls by males or nonterritorial female calls were likely to be detected on a weekly basis. When we extrapolated station-level detection probabilities to the equivalent of a hexagon with five stations using the power formula $p_{hexagon} = 1 - (1 - p_{station})^5$, the probability of detecting spotted owls at one or more stations within a hexagon in a weekly period $p_{hexagon}$ was approximately 0.17 in hexagons with nonpaired owls, 0.60 in hexagons with pairs, and 0.15 for the detection and correct classification of pairs. Further extending the power formula for repeat surveys, in hexagons surveyed with five ARU stations, we expect that the probability of detecting any spotted owl at a hexagon occupied by a pair would be 0.98 by week 4 of a survey, whereas the probability of detecting and correctly classifying a pair at a hexagon occupied by a pair would be 0.72 with 8 weeks of surveys (Appendix S3: Figure S1).

The model for inference on covariate effects included additive effects of NOISE and EFFORT on p and additive effects of STUDY_AREA, NR_SUIT_{500m}, and BO_{total} on both ψ and R. Parameter estimates from models with the three sets of prior probabilities that we tested were in close agreement (Appendix S4), so for interpretation, we used the model with priors Normal $(\mu = 0, \tau = 0.368)$.

We interpreted the omission of SEASON, BO_{weekly}, and $NR\_SUIT\_STN_{200m}$ during model selection as evidence that these covariates were not related to detection probability for spotted owls (Table 2) but we interpreted the effects of NOISE and EFFORT, which were retained, from the full model (Table 4). According to these estimates, the probability of detecting spotted owls at a station during a survey

TABLE 3 Derived parameter estimates from the most supported model following sequential-by-submodel selection to estimate multistate landscape use, pair occupancy, and detection probability for northern spotted owls in the Oregon Coast Range and Olympic Peninsula, using detections from passive acoustic monitoring in 2018. Detection probabilities are for one station–week survey period.

Derived parameter	Description	Mean	SD	95% LCI	95% UCI
Detection					
p_1	Probability of detecting spotted owls in hexagons with landscape use	0.037	0.011	0.020	0.062
p_2	Probability of detecting spotted owls in hexagons with pair occupancy	0.169	0.022	0.129	0.214
δ	Probability of detecting evidence of pair in hexagons with pair	0.188	0.048	0.109	0.292
p_{pair}[a]	Probability of detecting spotted owl pair	0.032	0.010	0.017	0.054
Occupancy					
ψ	Probability that a hexagon is used by spotted owls	0.206	0.035	0.143	0.282
R	Probability that spotted owls are paired given that a hexagon is used	0.361	0.091	0.195	0.548
$\psi_{nonpair}$[b]	Probability that a hexagon is used but not occupied by a pair	0.132	0.031	0.078	0.200
ψ_{pair}[c]	Probability that a hexagon is used and occupied by a pair	0.074	0.021	0.037	0.119
ψ_{unused}[d]	Probability that a hexagon is not used by spotted owls	0.794	0.035	0.718	0.857

Note: Shown are the mean, standard deviation (SD), and lower and upper 95% credible intervals (CI) of the inverse-logit-transformed posterior distributions for the intercept(s) of each parameter. Estimates are from a model with additive effects of background noise and recording effort on p_1 and p_2 and intercept-only structure on δ, ψ, and R.

[a] $p_2 \times \delta$.

[b] $\psi \times (1-R)$.

[c] $\psi \times R$.

[d] $1-\psi$.

week, given that a pair was present in the hexagon and available for detection, decreased from approximately 0.45 at station-weeks with the minimum level of NOISE to 0.16 at station-weeks with the mean NOISE level of −103 dBFS (Figure 3). In hexagons with landscape use only, detection probabilities at station-weeks with the minimum and mean NOISE levels were approximately 0.13 and 0.03, respectively (Figure 3). At the noisiest station-weeks (> −80 dBFS), detection probability approached 0 for hexagons in both occupancy states. At our expected level of EFFORT (3360 min/week), detection probability at ARU stations was approximately 0.19 in hexagons with pairs and 0.04 in hexagons with landscape use only (Figure 3).

We estimated probabilities of 0.89 and 0.95 that NR_SUIT_{500m} was positively related to ψ and R, respectively, although these effects were relatively weak with low precision (Table 4; Figure 4). The effects of BO_{total} were negative but also had low precision, with only a 0.69 probability that the effect on ψ was negative but a 0.89 probability that the effect on R was negative (Table 4; Figure 4). Finally, we did not detect a difference in STUDY_AREA for either ψ or R, with a high degree of overlap of the CIs (Table 4; Figure 5). These relatively weak effects were expected because no covariates were retained on the occupancy parameters during the submodel selection process (Table 2).

We estimated $\Pr(\text{site occuped by pair} | \text{any owl detected}) = 0.72$, suggesting that when any owl was detected at an ARU station, it was highly likely that the owl belonged to a pair. The probability of use in hexagons with no detections ψ_{cond} was estimated to be 0.06, and the proportion of hexagons used $\hat{\psi}$ was estimated to be 0.21.

DISCUSSION

Passive acoustic monitoring and multistate occupancy modeling are two active areas of research that are increasingly being used for rare, threatened, and wide-ranging species. We demonstrated that coupling these methods can be effective for monitoring imperiled northern spotted owl populations. Further, by incorporating sex-specific predictions into our observations, we were able to infer potential pair status and thus propose a method for distinguishing estimates of landscape use from pair occupancy, along with weekly detection

TABLE 4 Parameter estimates from the fully parameterized model to estimate multistate landscape use, pair occupancy, and detection probability for northern spotted owls in the Oregon Coast Range and Olympic Peninsula, using detections from passive acoustic monitoring in 2018.

Parameter	Mean	SD	95% LCI	95% UCI	*F*-score[a]	Odds ratio[b]	Odds ratio 95% LCI	Odds ratio 95% UCI
Use (ψ)								
Intercept	−1.551	0.351	−2.249	−0.865	1.000	...	...	...
NR_SUIT_{500m}	0.263	0.214	−0.155	0.688	0.892	1.298	0.856	1.989
STUDY_AREA	0.231	0.449	−0.644	1.115	0.696	1.259	0.525	3.048
BO_{total}	−0.113	0.220	−0.568	0.297	0.689	0.900	0.567	1.346
Probability of being paired (*R*)								
Intercept	−0.128	0.794	−1.616	1.520	0.581	...	...	...
NR_SUIT_{500m}	0.869	0.567	−0.134	2.087	0.952	2.296	0.874	8.063
STUDY_AREA	−0.852	0.890	−2.651	0.852	0.833	0.435	0.071	2.344
BO_{total}	−0.606	0.525	−1.758	0.286	0.891	0.573	0.172	1.332
Detection probability								
Intercept for nonpair (p_1)	−3.416	0.283	−3.991	−2.883	1.000	...	...	...
Intercept for pair (p_2)	1.750	0.280	1.211	2.310	1.000	...	...	...
NOISE	−0.725	0.130	−0.984	−0.472	1.000	0.485	0.374	0.624
EFFORT	0.431	0.158	0.146	0.764	0.999	1.525	1.158	2.148
Detection probability for evidence of pair (δ)								
Intercept	−1.559	0.292	−2.147	−1.002	1.000	...	...	...

Note: Posterior means, standard deviations (SD), and lower and upper 95% credible intervals (CI) are presented, along with *F*-scores and odds ratios. Estimates are from a model with additive effects of background noise (NOISE) and recording effort (EFFORT) on p_1 and p_2, an intercept-only structure on δ, and additive effects of nesting–roosting forest suitability at a 500-m scale (NR_SUIT_{500m}), study area, and total amount of barred owl detections (BO_{total}) on ψ and *R*.
[a]Proportion of the posterior distribution <0 or >0.
[b]Odds ratios were calculated as the median of the exponentiated posterior draws.

probabilities for paired and nonpaired spotted owls. This approach also allowed us to investigate the effects of barred owl calling intensity, suitability of forest cover for spotted owl nesting and roosting, and other hexagon- and survey-level characteristics on spotted owl landscape use, pair occupancy, and detection probabilities.

Occupancy models directly estimate the true biological states by accounting for imperfect detection in the sampling process, which is critical for making informed inference from analysis of detection/nondetection data (Nichols et al., 2007). These considerations are particularly important for developing survey design and management benchmarks for spotted owls. Management decisions that affect habitat protection from timber harvest may be based on occupancy status of spotted owls that are nonresidents, resident singles, or pairs. We estimated that the rate of hexagon occupancy by pairs was between 1.3 and 4.1 times greater than the proportion of hexagons where a female and male were both detected, so the true number of pairs would be far undercounted without adjusting for imperfect detection.

Given the sensitivity of spotted owls to land management decisions, it is critical that survey methods—especially those designed to inform protection levels by determining pair status—account for imperfect detection of pairs, which are the most important biological unit in need of protection. The probability of detecting and classifying a pair where present (0.03 at a single station and week) was quite low and suggests that a requirement for detecting both female and male owls to determine pair status with high confidence would require an extensive and onerous survey effort and may be unachievable. We suggest that single detections could be used as an alternative benchmark to ensure protection of sites used by spotted owl pairs. Stations in hexagons with potential spotted owl pairs had the highest weekly detection probability (0.169), most likely driven by males exhibiting more active calling behavior in territorial defense when paired. This pattern of higher detectability for paired owls has been observed previously (Duchac et al., 2020; Tempel & Gutiérrez, 2013). Conversely, stations in hexagons with only species-level landscape use by spotted owls had low detection probability (0.037), suggesting that affording protections to any site with spotted owl detections would rarely result in protecting sites used only by nonresident spotted owls. Using callback surveys, Olson et al. (2005)

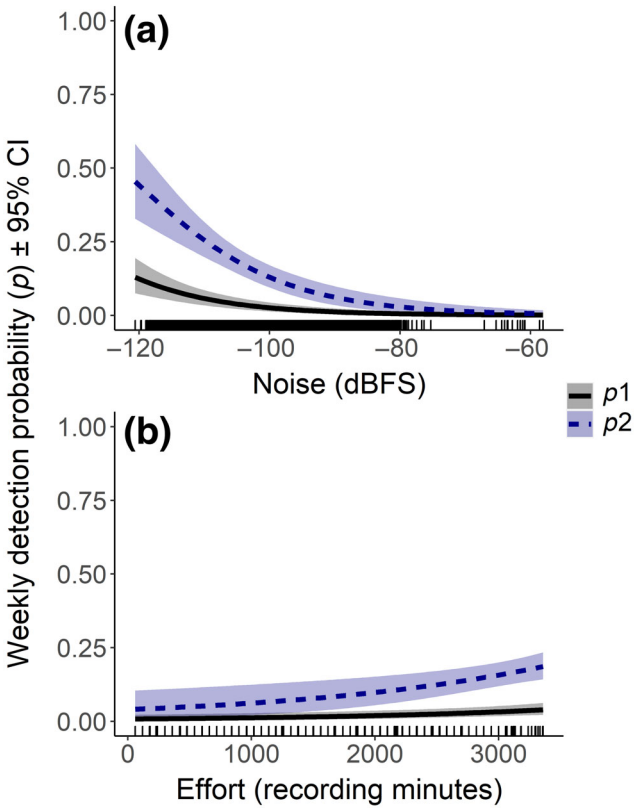

FIGURE 3 Marginal plots relating the probability of detecting spotted owls (p) with (a) the level of mean weekly background noise (decibels below full scale [dBFS]) and (b) total weekly recording effort (in minutes) at autonomous recording unit stations for passive acoustic monitoring in the Oregon Coast Range and Olympic Peninsula in 2018. Shading represents 95% credible intervals (CI). Detection probability was modeled with different intercepts for stations in survey hexagons (5 km^2) occupied by spotted owl pairs (p_2) and hexagons with only species-level landscape use (p_1), but the slope coefficients were shared. Ticks on the x-axis represent real values of weekly noise and recording effort measured at stations used for the analysis. Estimates are from a multistate occupancy model with additive effects of background noise and recording effort on detection probabilities p_1 and p_2, an intercept-only structure on δ, and additive effects of nesting–roosting forest suitability at a 500-m scale and total amount of barred owl detections on ψ and R.

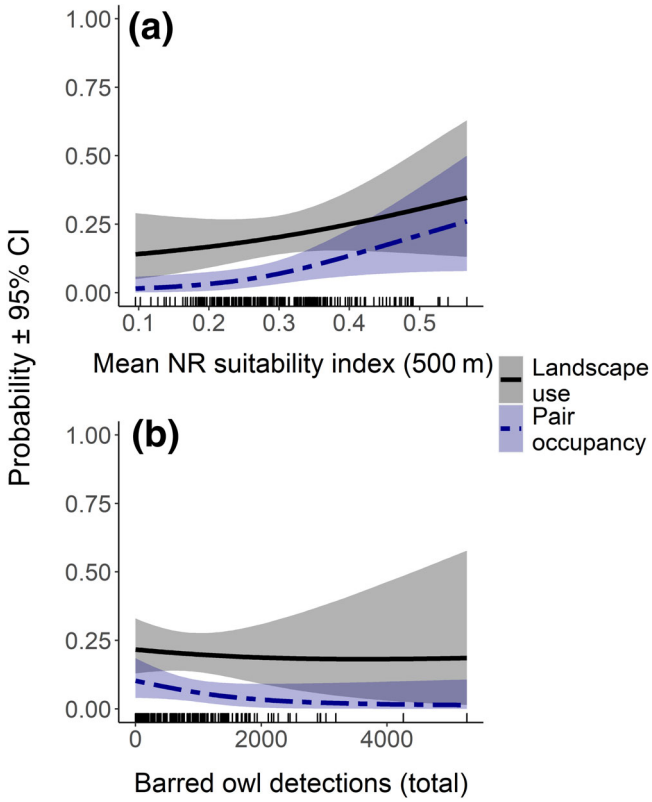

FIGURE 4 Marginal plots relating the probability of landscape use by spotted owls (ψ) and the probability of pair occupancy (ψ_{pair}) with two environmental variables using data from passive acoustic monitoring in the Oregon Coast Range and Olympic Peninsula in 2018. Shading represents 95% credible intervals (CI). Ticks on the x-axis represent real values of (a) nesting–roosting (NR) forest suitability within 500-m buffers of all autonomous recording unit stations within a 5-km^2 survey hexagon and (b) the total amount of barred owl detections recorded in each hexagon. Estimates are from a multistate occupancy model with additive effects of background noise and recording effort on detection probabilities p_1 and p_2, an intercept-only structure on δ, and additive effects of NR suitability and total barred owl detections on ψ and R.

estimated detection probability for spotted owl pairs as 0.51 (with a range of 0.22–0.67 across all study areas) in historical territories, resulting in approximately 0.97 detection probability for pairs after five visits. For owl pairs, we found a similar detection probability with 4–5 weeks of sampling and 4–5 stations per hexagon (Appendix S3: Figure S1). We agree with Olson et al. (2005) that these detection probabilities are sufficient for many studies, but the consequences of missing a pair or of misidentifying a pair as a single owl are high when management actions are dependent on correctly classifying states. Using only naïve survey results and requiring both sexes to be detected as the basis of pair determinations would likely result in loss of habitat and be detrimental for spotted owl pairs.

Female spotted owls call less frequently than males, especially away from the nest and using the 4-note hoot (Ganey, 1990; Reid et al., 1999; Wood, Schmidt, et al., 2019); therefore, female calling behavior is important to consider when determining pair status. Reid et al. (1999) found that male spotted owls were more than twice as detectable as females using the commonly employed 10-min nighttime callback protocol designed to detect territorial owls (Franklin et al., 1996). Using passive acoustic monitoring, we detected female 4-note calls only

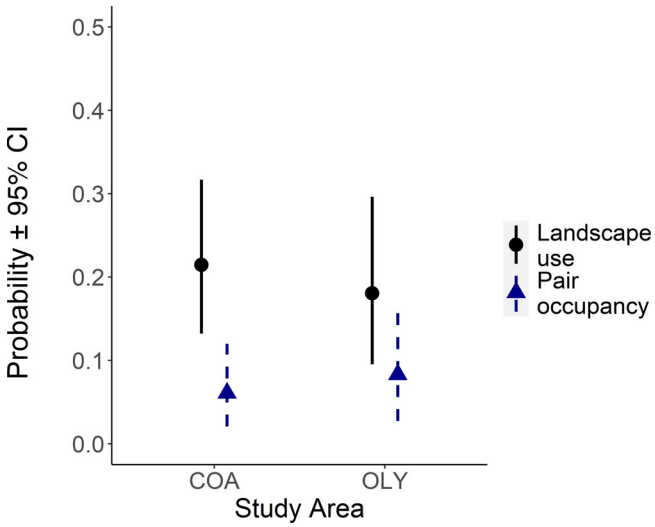

FIGURE 5 Marginal plot comparing the probability of landscape use by spotted owls (ψ) and the probability of pair occupancy (ψ_{pair}) in the Oregon Coast Range (COA) and Olympic Peninsula (OLY) study areas using data from passive acoustic monitoring in 2018. Error bars represent 95% credible intervals (CI). Estimates are from a multistate occupancy model with additive effects of background noise and recording effort on detection probabilities p_1 and p_2, an intercept-only structure on δ, and additive effects of nesting–roosting forest suitability at a 500-m scale, study area, and total amount of barred owl detections on ψ and *R*.

in hexagons where males were also detected. Previous studies provided evidence that females are less responsive to broadcasted conspecific calls. By observing natural calling behavior, we found that females were less likely to call than males even without human attempts to elicit a territorial response. Passive acoustic monitoring eliminates any bias related to individual behavioral responses to human-broadcasted conspecific calls and thus provides deeper insights into natural calling behaviors of spotted owls.

We found near-complete overlap of hexagons used by spotted owls and the presence of barred owls, with barred owls detected in 92% of our surveyed hexagons in OLY and 100% of our surveyed hexagons in COA. Of the seven hexagons in OLY with no barred owl detections, spotted owls were detected in two, although these were not confirmed 4-note calls by females. These findings are similar to occupancy estimates derived from incidental barred owl detections during spotted owl surveys in historical territories (Franklin et al., 2021; Yackulic et al., 2019), barred owl-specific callback surveys in 5-km^2 hexagons (Wiens et al., 2020, 2021), and previous passive acoustic monitoring (Duchac et al., 2020). Pairing passive acoustic monitoring with identification of calls using the PNW-Cnet allowed us to obtain unbiased detections of barred owls and spotted owls across the entire landscape, not just within historical spotted owl territories. Hexagons were selected randomly with respect to habitat for both species, and barred owls have multiple stereotyped calls that the PNW-Cnet performed well in identifying (Ruff et al., 2021). Previous passive acoustic monitoring studies have found high detection probabilities and occupancy rates for barred owls in the region (Duchac et al., 2020) but lower occupancy rates in post-wildfire areas (Duchac et al., 2021). Because barred owls have high detection probability and were ubiquitous in our study areas, we modeled the intensity of barred owl calling to test whether heterogeneity in the amount of barred owl detections affected spotted owl detection, landscape use, and occupancy probabilities. We believe it was reasonable to expect that spotted owls may respond to the intensity of barred owl vocal activity, not just presence or absence of barred owls, as these calls are used for territorial defense and interspecific competition. We estimated that there was a 0.89 probability that spotted owls were less likely to be paired when using hexagons with high amounts of barred owl calling activity, which is consistent with evidence that competition by barred owls may suppress spotted owl recruitment and other demographic rates (Franklin et al., 2021; Rockweit et al., 2022; Wiens et al., 2021). We found no effect of barred owl calling intensity on detection probability of spotted owls and only weak evidence of a negative effect on the probability of landscape use. The inconsistent effect of barred owl calling intensity may mean that spotted owls are affected by the presence of barred owls, and not necessarily the intensity of calling, through competitive interactions (e.g., Van Lanen et al., 2011).

Spotted owls require large trees in old forests with tall, closed canopies for nesting and roosting (Sovern et al., 2019; Wilk et al., 2018). These areas provide cavities, platforms, and other structures that spotted owls use for nesting, as well as suitable microclimates for thermoregulation and habitat for small mammals that comprise the owls' prey base (e.g., Forsman et al., 1984; Sovern et al., 2019). Predictions of suitable NR sites using forest structure and composition data have been shown to correlate closely with the distribution and density of spotted owl territories (Glenn et al., 2017). Old forests in the Pacific Northwest are also used by barred owls, although recent evidence suggests fine-scale resource partitioning between the two species (Jenkins, Lesmeister, Wiens, et al., 2019). We incorporated a covariate of NR forest suitability to ensure that the effects of other covariates, such as barred owl calling intensity, were not confounded by underlying selection of suitable sites by spotted owls. Our study provided evidence that spotted owls were more likely to be present—and more likely to be paired when

present—in hexagons with higher levels of suitable NR forest cover, although the effects were weak with low precision. We predicted this relationship but were unsure if it would be a finding in our analysis because most of the areas surveyed were protected as late-successional forest reserves under the Northwest Forest Plan, so most of our hexagons had forests that were at least moderately suitable for nesting and roosting. Additionally, the occurrence of spotted owls may be increasingly decoupled from forest suitability due to displacement by barred owls, resulting in areas with highly suitable forest being currently unoccupied. Nevertheless, these and other recent findings (Franklin et al., 2021; Wiens et al., 2021) suggest that preserving forests with stand characteristics suitable for spotted owl nesting and roosting is essential for their persistence and any future recovery.

Depending on study objectives, placement of ARUs in specific cover types is a common concern when creating a survey design for passive acoustic monitoring. In our study, the detection of spotted owls within a hexagon was not affected by the suitability of forest for nesting and roosting, suggesting that deploying ARUs only in highly suitable forest cover is not necessary to achieve a robust detection probability (e.g., ≥0.95). However, conducting surveys at multiple stations within hexagons (i.e., multiple spatial replicates) was important for achieving high cumulative detection probability. Our sampling included five ARU stations in each hexagon, and in 79% of the hexagons where we detected spotted owls, we detected them at only one or two stations, demonstrating the importance of spatial replication within hexagons. Hexagons were selected randomly from a space-filling grid, so in most cases, they overlapped only a portion of a spotted owl's established territory. We recognize the potential for unequal availability for detection among ARU stations, further highlighting the strength of the multistate framework (landscape use and pair occupancy) and the need to have multiple ARUs in each hexagon with placement not determined by the suitability of forest for nesting and roosting. Future efforts may explicitly model the relationship between station-level detection and hexagon-level occupancy processes with a multistate, multiscale approach, but to our knowledge these models have only been explored preliminarily (Kleiven et al., 2021).

Detection of spotted owls was negatively affected by increasing levels of background noise, as has been found previously (Duchac et al., 2020). Extracting patterns of interest from spectrograms with low signal-to-noise ratio due to persistent noise is difficult. Background noise from wind, rain, and other natural and anthropogenic sources is a challenge for any auditory survey method, but the ability to extract noise information from acoustic recordings and explicitly model its effect provides a distinct advantage over human-observer surveys. Nevertheless, when deploying ARUs, precautions are needed to minimize background noise by placing recorders away from roads, streams, and other sources of noise, where possible. Replication of surveys across time and space will also decrease the likelihood of failing to detect owls when present due to intermittent background noise events such as wind and rain. Importantly, after accounting for the influence of background noise, we found no difference in detectability between surveys in the late season compared with the early season, further evidence that passive acoustic monitoring will reliably detect spotted owls throughout the breeding period (Duchac et al., 2020).

Classification of calls by sex is an important advancement toward extracting demographic information from acoustic recordings and adds crucial detail beyond species-level detection/nondetection data (Dale et al., 2022). We were able to accurately classify 95% of our test dataset containing high-quality recordings of 4-note calls. However, approximately half of the spotted owl calls we recorded were either low quality or were not 4-note hoots, which we were unable to classify to sex. Here, low quality refers to recordings with a low signal-to-noise ratio, which can result from owls vocalizing far away from the ARU, low call volume, high background noise, or topographic interference. There is a distance threshold at which calls become unidentifiable (Hane et al., 2022; Maegawa et al., 2021). Nevertheless, the Dale et al. (2022) model performed well for calls that were clear enough to generate predictions and offers a valuable step that can be integrated into a workflow for processing acoustic recordings.

We used detections of female spotted owls to define our highest occupancy state because females were never detected in hexagons where males were not also present. Additionally, territorial, resident females have been considered the target population for previous population estimates (Franklin et al., 1996). Although detections of female and male owls in spatial and temporal proximity may not always represent a reproductive pair, these uncertainties in reproductive status are not unique to acoustic monitoring methods. Dale et al. (2022) summarized the differences in call type proportions among sites where spotted owls were visually confirmed to be single, paired, and nesting, suggesting that call type may be informative for further classifying the reproductive status of owls using acoustic detections. All birds use a complex variety of calls and sounds in distinct circumstances, so further research into interpreting these vocalizations will continue the advancement of passive acoustic monitoring for studying increasingly imperiled spotted owl populations. Development of automated methods to identify specific call types that are indicative of reproductive behavior could

increase options for population analyses—for example, any detection of a spotted owl nest call or juvenile call is evidence of reproduction. Alternatively, the multistate model could be expanded to include additional states representing detections of singles, pairs, and pairs with successful reproduction.

In most parts of their range, northern spotted owls have declined to less than 35% of their pre-1995 population levels and face extirpation unless drastic management actions are undertaken (Franklin et al., 2021). As their populations continue to decline, northern spotted owls are making more frequent and longer dispersal movements (Jenkins et al., 2021; Jenkins, Lesmeister, Forsman, et al., 2019), which can further destabilize the population and contribute positive feedback to rapid population decline. Spotted owls are likely to continue to become less abundant and less widely distributed on the landscape, increasing their susceptibility to stochastic events such as wildfire that will lead to local extirpations and carry the subspecies further toward extinction (Franklin et al., 2021; Hanski, 1998)—a "double jeopardy" problem for rare and declining species (Gaston et al., 2000).

The number of northern spotted owl breeding pairs on the landscape is very low and steadily declining (Davis et al., 2022), highlighting the need to protect habitat occupied by pairs. However, detecting both members of a pair is difficult—due mostly to infrequent calling by females—suggesting that pairs may often go undetected even after repeated sampling. When determining pair or residency status is necessary for assigning appropriate protections, the observed presence of a female and male to define pair status may be a threshold too high and unachievable to ensure that areas used by breeding owls are adequately protected. In fact, we found that hexagons with only landscape use detected likely represented undetected spotted owl pairs in nearly three out of four cases. Further consideration will be needed to weigh the likelihood and acceptable level of risk associated with errors of omission or commission. For example, falsely classifying sites as not occupied by a pair may result in insufficient protections. Less probable would be falsely classifying a site as used by a resident owl when the site is used by a nonresident owl. The commission error of protecting a site with nonresident owl detections may have an unintended benefit by maintaining forest structure at a site that will be suitable for occupancy by spotted owl pairs in the future.

With the transition to passive acoustic monitoring, future analyses will need to adapt to a modeling framework based on spotted owl occupancy and a stronger linkage to USDA forest inventory data (Lesmeister & Jenkins, 2022). Therefore, understanding the relationships between landscape use, pair occupancy, and abundance for spotted owls will be critical to detect population changes accurately and rapidly. We demonstrated how distinguishing the sex of owls can be used to estimate state-specific detection and occupancy rates, an important step beyond species-level detection/nondetection. Data from overlapping years of using both mark–resight and passive acoustic monitoring methods will be valuable for interpreting the biological state of owls based on detections of calls. For example, understanding calling behavior by spotted owls away from their territory centers will allow for distinguishing between detections of resident pairs and incursions from neighboring or transient owls, which will reduce double counting of owls and improve bias in estimates of occupancy in relation to underlying changes in the population (Berigan et al., 2019; Lesmeister et al., 2021; Reid et al., 2021). Further, development of methods to individually identify owls based on vocal characteristics is an area of active research (Bistel et al., 2021; Wood et al., 2021; Zhou et al., 2020) and would approximate estimates from mark–resight analyses (Terry et al., 2005). In addition to filtering detections of nonterritorial owls, individual identification could also be used to track between-season movements of breeding owls, which are becoming increasingly common (Jenkins et al., 2021). With multiple years of data, our methods may be extended using a dynamic multistate modeling approach to directly estimate the probability of sites transitioning between paired and unpaired states (e.g., MacKenzie et al., 2009). Overall, passive acoustic monitoring coupled with remotely sensed forest data shows great promise for spotted owl conservation and management, especially when combined with automated workflows to allow rapid processing of data and further methods to extract information on owl sex and pair status. These and future developments will permit accurate and timely detection of changes in spotted owl populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code to fit the models (Appel, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.7530362.

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REFERENCES

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, et al. 2006. "Status and Trends in Demography of Northern Spotted Owls, 1985–2003." *Wildlife Monographs* 163: 1–48. https://doi.org/10.2193/0084-0173(2006)163[1:satido]2.0.co;2.

Appel, C. L. 2023. "appelc/multistate-owl-models (v1.1)." Zenodo. Dataset. https://doi.org/10.5281/zenodo.7530362.

Araya-Salas, M., and G. Smith-Vidaurre. 2017. "WarbleR: An R Package to Streamline Analysis of Animal Acoustic Signals." *Methods in Ecology and Evolution* 8(2): 184–91. https://doi.org/10.1111/2041-210X.12624.

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2019. "Cryptic Wide-Ranging Movements Lead to Upwardly Biased Occupancy in a Territorial Species." *Journal of Applied Ecology* 56(2): 470–80. https://doi.org/10.1111/1365-2664.13265.

Bistel, R. A., A. Martinez, and G. B. Mindlin. 2021. "Neural Networks That Locate and Identify Birds through Their Songs." *The European Physical Journal* 123: 10. https://doi.org/10.1140/epjs/s11734-021-00405-5.

Brooks, S. P., and A. Gelman. 1998. "General Methods for Monitoring Convergence of Iterative Simulations." *Journal of Computational and Graphical Statistics* 7(4): 434–55.

Campos-Cerqueira, M., and T. M. Aide. 2016. "Improving Distribution Data of Threatened Species by Combining Acoustic Monitoring and Occupancy Modelling." *Methods in Ecology and Evolution* 7(11): 1340–8. https://doi.org/10.1111/2041-210X.12599.

Conner, M. M., J. J. Keane, C. V. Gallagher, T. E. Munton, and P. A. Shaklee. 2016. "Comparing Estimates of Population Change from Occupancy and Mark-Recapture Models for a Territorial Species." *Ecosphere* 7(10): e01538. https://doi.org/10.1002/ecs2.1538.

Dale, S. S., J. M. A. Jenkins, Z. J. Ruff, L. S. Duchac, C. E. McCafferty, and D. B. Lesmeister. 2022. "Distinguishing Sex of Northern Spotted Owls with Passive Acoustic Monitoring." *Journal of Raptor Research* 56(3): 287–99. https://doi.org/10.3356/JRR-21-33%0A.

Davis, R. J., D. B. Lesmeister, Z. Yang, B. Hollen, B. Tuerler, J. Hobson, J. Guetterman, and A. Stratton. 2022. *Northwest Forest Plan—The First 25 Years (1994–2017): Status and Trends of Northern Spotted Owl Habitats*. General Technical Report PNW-GTR-1003. Portland, OR: USDA Forest Service. https://doi.org/10.2737/PNW-GTR-1003.

Davis, R. J., J. L. Ohmann, R. E. Kennedy, W. B. Cohen, M. J. Gregory, Z. Yang, H. M. Roberts, A. N. Gray, and T. A. Spies. 2015. *Northwest Forest Plan—The First 20 Years (1994–2013): Status and Trends of Late-Successional and Old-Growth Forests*. General Technical Report PNW-GTR-911. Portland, OR: USDA Forest Service. https://doi.org/10.2737/PNW-GTR-911.

Duarte, A., and J. T. Peterson. 2021. "Space-for-Time Is Not Necessarily a Substitution When Monitoring the Distribution of Pelagic Fishes in the San Francisco Bay-Delta." *Ecology and Evolution* 11(23): 16727–44. https://doi.org/10.1002/ece3.8292.

Duarte, A., J. T. Peterson, C. A. Pearl, J. C. Rowe, B. McCreary, S. K. Galvan, and M. J. Adams. 2020. "Estimation of Metademographic Rates and Landscape Connectivity for a Conservation-Reliant Anuran." *Landscape Ecology* 35(6): 1459–79. https://doi.org/10.1007/s10980-020-01030-8.

Duchac, L. S. 2019. "Passive Acoustic Monitoring of Owls: Two Studies in Forested Landscapes of the Pacific Northwest." MS thesis, Oregon State University.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, and R. J. Davis. 2021. "Differential Landscape Use by Forest Owls Two Years after a Mixed-Severity Wildfire." *Ecosphere* 12(10): e03770. https://doi.org/10.1002/ecs2.3770.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, Z. J. Ruff, and R. J. Davis. 2020. "Passive Acoustic Monitoring Effectively Detects Northern Spotted Owls and Barred Owls over a Range of Forest Conditions." *The Condor* 122: 1–22. https://doi.org/10.1093/condor/duaa017.

Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J. Schwarz, K. P. Burnham, et al. 2016. "The Effects of Habitat, Climate, and Barred Owls on Long-Term Demography of Northern Spotted Owls." *The Condor* 118(1): 57–116. https://doi.org/10.1650/condor-15-24.1.

Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, et al. 2011. *Population Demography of Northern Spotted Owls*. Studies in Avian Biology 40, Published for the Cooper Ornithological Society. Berkeley, CA: University of California Press. https://doi.org/10.1525/9780520950597.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. "Distribution and Biology of the Spotted Owl in Oregon." *Wildlife Monographs* 87: 3–64. https://www.jstor.org/stable/3830695.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner. 1996. "Methods for Collecting and Analyzing Demographic Data on the Northern Spotted Owl." *Condor* 98(17): 12–20.

Franklin, A. B., K. M. Dugger, D. B. Lesmeister, R. J. Davis, J. D. Wiens, G. C. White, J. D. Nichols, et al. 2021. "Range-Wide Declines of Northern Spotted Owl Populations in the Pacific Northwest: A Meta-Analysis." *Biological Conservation* 259: 109168. https://doi.org/10.1016/j.biocon.2021.109168.

Fuller, A. K., B. C. Augustine, D. J. Morin, K. Pigeon, J. Boulanger, D. C. Lee, F. Bisi, and D. L. Garshelis. 2022. "The

Occupancy-Abundance Relationship and Sampling Designs Using Occupancy to Monitor Populations of Asian Bears." *Global Ecology and Conservation* 35: e02075. https://doi.org/10.1016/j.gecco.2022.e02075.

Ganey, J. L. 1990. "Calling Behavior of Spotted Owls in Northern Arizona." *The Condor* 92(2): 485–90. https://doi.org/10.2307/1368245.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. "Abundance-Occupancy Relationships." *Journal of Applied Ecology* 37: 39–59. https://doi.org/10.1046/j.1365-2664.2000.00485.x.

Glenn, E. M., D. B. Lesmeister, R. J. Davis, B. Hollen, and A. Poopatanapong. 2017. "Estimating Density of a Territorial Species in a Dynamic Landscape." *Landscape Ecology* 32(3): 563–79. https://doi.org/10.1007/s10980-016-0467-6.

Hane, M. E., J. E. Thornton-Frost, A. Springford, and A. J. Kroll. 2022. "Factors Associated with Automated Detection of Northern Spotted Owl (*Strix occidentalis caurina*) Four-Note Location Calls." *Avian Conservation and Ecology* 17(1): 26. https://doi.org/10.5751/ace-02105-170126.

Hanski, I. 1998. "Metapopulation Dynamics." *Nature* 396: 41–9. https://doi.org/10.1038/23876.

Jenkins, J. M. A., D. B. Lesmeister, J. D. Wiens, J. T. Kane, V. R. Kane, and J. Verschuyl. 2019. "Three-Dimensional Partitioning of Resources by Congeneric Forest Predators with Recent Sympatry." *Scientific Reports* 9: 6036. https://doi.org/10.1038/s41598-019-42426-0.

Jenkins, J. M. A., D. B. Lesmeister, E. D. Forsman, K. M. Dugger, S. H. Ackers, L. S. Andrews, S. A. Gremel, et al. 2021. "Conspecific and Congeneric Interactions Shape Increasing Rates of Breeding Dispersal of Northern Spotted Owls." *Ecological Applications* 31(7): e02398. https://doi.org/10.1002/eap.2398.

Jenkins, J. M. A., D. B. Lesmeister, E. D. Forsman, K. M. Dugger, S. H. Ackers, L. S. Andrews, C. E. McCafferty, et al. 2019. "Social Status, Forest Disturbance, and Barred Owls Shape Long-Term Trends in Breeding Dispersal Distance of Northern Spotted Owls." *The Condor: Ornithological Applications* 121(4): 1–17. https://doi.org/10.1093/condor/duz055.

Jiménez, J., J. C. Nuñez-Arjona, C. Rueda, L. M. González, F. Garciá-Domínguez, J. Munõz-Igualada, and J. V. López-Bao. 2017. "Estimating Carnivore Community Structures." *Scientific Reports* 7: 41036. https://doi.org/10.1038/srep41036.

Kellner, K. 2019. "JagsUI: A Wrapper around 'rjags' to Streamline 'JAGS' Analyses." R Package Version 1.5.1. https://cran.r-project.org/package=jagsUI.

Kéry, M., and J. A. Royle. 2016. In *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS. Volume 1: Prelude and Static Models*, edited by J. A. Royle, 71–2. Amsterdam: Elsevier Academic Press.

Kleiven, E. F., F. Barraquand, O. Gimenez, J.-A. Henden, R. A. Ims, E. M. Soininen, and N. G. Yoccoz. 2021. "A Dynamic Occupancy Model for Interacting Species with Two Spatial Scales." bioRxiv. 2021. https://doi.org/10.1101/2020.12.16.423067.

Kuo, L., and B. Mallick. 1998. "Variable Selection for Regression Models." *Sankhyā: The Indian Journal of Statistics, Series B* 60(1): 65–81.

Lesmeister, D. B., C. L. Appel, R. J. Davis, C. B. Yackulic, and Z. J. Ruff. 2021. *Simulating the Effort Necessary to Detect Changes in Northern Spotted Owl (Strix occidentalis caurina) Populations Using Passive Acoustic Monitoring. Research Paper PNW-RP-618*. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. https://www.fs.usda.gov/research/treesearch/62862.

Lesmeister, D. B., R. J. Davis, L. S. Duchac, and Z. J. Ruff. 2019. *Northern Spotted Owl Passive Acoustic Monitoring 2018 Annual Report*. Corvallis, OR: USDA Forest Service, Pacific Northwest Research Station.

Lesmeister, D. B., R. J. Davis, P. H. Singleton, and J. D. Wiens. 2018. "Northern Spotted Owl Habitat and Populations: Status and Threats." In *Synthesis of Science to Inform Land Management within the Northwest Forest Plan Area*. General Technical Report PNW-GTR-966, edited by T. A. Spies, P. A. Stine, R. Gravenmier, J. W. Long, and M. J. Reilly, 245–99. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-966.

Lesmeister, D. B., and J. M. A. Jenkins. 2022. "Integrating New Technologies to Broaden the Scope of Northern Spotted Owl Monitoring and Linkage with USDA Forest Inventory Data." *Frontiers in Forests and Global Change* 5: 966978. https://doi.org/10.3389/ffgc.2022.966978.

Lesmeister, D. B., J. M. A. Jenkins, Z. J. Ruff, R. J. Davis, C. L. Appel, A. D. Thomas, S. Gremel, et al. 2022. *Passive Acoustic Monitoring within the Northwest Forest Plan Area: 2021 Annual Report*. Corvallis, OR: USDA Forest Service, Pacific Northwest Research Station.

Lint, J. B., B. R. Noon, R. G. Anthony, E. D. Forsman, M. G. Raphael, M. Collopy, and E. E. Starkey. 1999. *Northern Spotted Owl Effectiveness Monitoring Plan for the Northwest Forest Plan*. General Technical Report PNW-GTR-440. Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2018. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*, 2nd ed. London: Elsevier Academic Press. https://doi.org/10.1016/C2012-0-01164-7.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. "Estimating Site Occupancy Rates When Detection Probabilities Are Less than One." *Ecology* 83(8): 2248–55. https://doi.org/10.2307/3072056.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. "Modeling Species Occurrence Dynamics with Multiple States and Imperfect Detection." *Ecology* 90(3): 823–35. https://doi.org/10.1890/08-0141.1.

Maegawa, Y., Y. Ushigome, M. Suzuki, K. Taguchi, K. Kobayashi, C. Haga, and T. Matsui. 2021. "A New Survey Method Using Convolutional Neural Networks for Automatic Classification of Bird Calls." *Ecological Informatics* 61: 101164. https://doi.org/10.1016/j.ecoinf.2020.101164.

Mitchell, T. J., and J. J. Beauchamp. 1988. "Bayesian Variable Selection in Linear Regression." *Journal of the American Statistical Association* 83(404): 1023–32. https://doi.org/10.1080/01621459.1988.10478694.

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber. 2020. "Is Your Ad Hoc Model Selection Strategy Affecting Your Multimodel Inference?" *Ecosphere* 11(1): e02997. https://doi.org/10.1002/ecs2.2997.

Nichols, J. D., J. E. Hines, D. I. MacKenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. "Occupancy Estimation and Modeling with Multiple States and State Uncertainty." *Ecology* 88(6): 1395–400. https://doi.org/10.1890/06-1474.

Norouzzadeh, M. S., A. Nguyen, M. Kosmala, A. Swanson, M. Palmer, C. Packer, and J. Clune. 2017. "Automatically Identifying, Counting, and Describing Wild Animals in Camera-Trap Images with Deep Learning." *Proceedings of the National Academy of Sciences of the United States of America* 115(25): E5717–25. https://doi.org/10.1073/pnas.1719367115.

Northrup, J. M., and B. D. Gerber. 2018. "A Comment on Priors for Bayesian Occupancy Models." *PLoS Biology* 13(2): e0192819. https://doi.org/10.1101/138735.

Odom, K. J., and D. J. Mennill. 2010. "A Quantitative Description of the Vocalizations and Vocal Activity of the Barred Owl." *The Condor* 112(3): 549–60. https://doi.org/10.1525/cond.2010.090163.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. "Modeling of Site Occupancy Dynamics for Northern Spotted Owls, with Emphasis on the Effects of Barred Owls." *Journal of Wildlife Management* 69(3): 918–32. https://doi.org/10.2193/0022-541x(2005)069[0918:mosodf]2.0.co;2.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, edited by K. Hornik, F. Leisch, and A. Zeileis, Vol. 124, 1–10. Vienna.

R Development Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. www.R-project.org/.

Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, J. J. Keane, S. C. Sawyer, P. A. Shaklee, et al. 2021. "Noisy Neighbors and Reticent Residents: Distinguishing Resident from Non-Resident Individuals to Improve Passive Acoustic Monitoring." *Global Ecology and Conservation* 28: e01710. https://doi.org/10.1016/j.gecco.2021.e01710.

Reid, J. A., R. B. Horn, and E. D. Forsman. 1999. "Detection Rates of Spotted Owls Based on Acoustic-Lure and Live-Lure Surveys." *Wildlife Society Bulletin* 27(4): 986–90.

Rockweit, J. T., J. M. A. Jenkins, J. E. Hines, J. D. Nichols, K. M. Dugger, A. B. Franklin, P. C. Carlson, et al. 2022. "Range-Wide Sources of Variation in Reproductive Rates of Northern Spotted Owls." *Ecological Applications* 33: e2726. https://doi.org/10.1002/eap.2726.

Ruff, Z. J., D. B. Lesmeister, C. L. Appel, and C. M. Sullivan. 2021. "Workflow and Convolutional Neural Network for Automated Identification of Animal Sounds." *Ecological Indicators* 124: 107419. https://doi.org/10.1016/j.ecolind.2021.107419.

Ruff, Z. J., D. B. Lesmeister, L. S. Duchac, B. K. Padmaraju, and C. M. Sullivan. 2019. "Automated Identification of Avian Vocalizations with Deep Convolutional Neural Networks." *Remote Sensing in Ecology and Conservation* 6(1): 79–92. https://doi.org/10.1002/rse2.125.

Shonfield, J., S. Heemskerk, and E. M. Bayne. 2018. "Utility of Automated Species Recognition for Acoustic Monitoring of Owls." *Journal of Raptor Research* 52(1): 42–55. https://doi.org/10.3356/JRR-17-52.1.

Sovern, S. G., D. B. Lesmeister, K. M. Dugger, M. S. Pruett, R. J. Davis, and J. M. Jenkins. 2019. "Activity Center Selection by Northern Spotted Owls." *Journal of Wildlife Management* 83(3): 714–27. https://doi.org/10.1002/jwmg.21632.

Steenweg, R., M. Hebblewhite, J. Whittington, P. Lukacs, and K. McKelvey. 2018. "Sampling Scales Define Occupancy and Underlying Occupancy–Abundance Relationships in Animals." *Ecology* 99(1): 172–83. https://doi.org/10.1002/ecy.2054.

Sugai, L. S., T. S. Moreira, F. Silva, J. W. Ribeiro, and D. Llusia. 2019. "Terrestrial Passive Acoustic Monitoring: Review and Perspectives." *Bioscience* 69(1): 15–25. https://doi.org/10.1093/biosci/biy147.

Tabak, M. A., M. S. Norouzzadeh, D. W. Wolfson, J. M. Halseth, S. J. Sweeney, K. C. Vercauteren, N. P. Snow, et al. 2019. "Machine Learning to Classify Animal Species in Camera Trap Images: Applications in Ecology." *Methods in Ecology and Evolution* 10: 585–90. https://doi.org/10.1111/2041-210X.13120.

Teixeira, D., M. Maron, and B. J. van Rensburg. 2019. "Bioacoustic Monitoring of Animal Vocal Behavior for Conservation." *Conservation Science and Practice* 1: e72. https://doi.org/10.1111/csp2.72.

Tempel, D. J., and R. J. Gutiérrez. 2013. "Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl." *Conservation Biology* 27(5): 1087–95. https://doi.org/10.1111/cobi.12074.

Terry, A. M. R., T. M. Peake, and N. P. K. McGregor. 2005. "The Role of Vocal Individuality in Conservation." *Frontiers in Zoology* 2: 10. https://doi.org/10.1186/1742-9994-2-10.

Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Norman Johnson. 2006. "The Northwest Forest Plan: Origins, Components, Implementation Experience, and Suggestions for Change." *Conservation Biology* 20(2): 277–87. https://doi.org/10.1111/j.1523-1739.2006.00385.x.

Tosa, M. I., E. H. Dziedzic, C. L. Appel, J. Urbina, A. Massey, J. Ruprecht, C. E. Eriksson, et al. 2021. "The Rapid Rise of Next-Generation Natural History." *Frontiers in Ecology and Evolution* 9: 1–18. https://doi.org/10.3389/fevo.2021.698131.

U.S. Fish and Wildlife Service. 2011. *Revised Recovery Plan for the Northern Spotted Owl (Strix occidentalis caurina)*. Portland, OR: U.S. Fish and Wildlife Service.

U.S. Fish and Wildlife Service. 2020. *Endangered and Threatened Wildlife and Plants; 12-Month Finding for the Northern Spotted Owl. Fed. Reg.* Vol. 85. Portland, OR: U.S. Fish and Wildlife Service.

Van Lanen, N. J., A. B. Franklin, K. P. Huyvaert, R. F. Reiser, and P. C. Carlson. 2011. "Who Hits and Hoots at Whom? Potential for Interference Competition between Barred and Northern Spotted Owls." *Biological Conservation* 144(9): 2194–201. https://doi.org/10.1016/j.biocon.2011.05.011.

Volodin, I. A., E. V. Volodina, A. V. Klenova, and V. A. Matrosova. 2015. "Gender Identification Using Acoustic Analysis in Birds without External Sexual Dimorphism." *Avian Research* 6(1): 6–20. https://doi.org/10.1186/s40657-015-0033-y.

Wei, T., and V. Simko. 2017. "R Package 'Corrplot': Visualization of a Correlation Matrix (Version 0.84)." https://github.com/taiyun/corrplot.

Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. "Competitive Interactions and Resource Partitioning between

Northern Spotted Owls and Barred Owls in Western Oregon." *Wildlife Monographs* 185: 1–50. https://doi.org/10.1002/wmon.1009.

Wiens, J. D., K. M. Dugger, J. M. Higley, D. B. Lesmeister, A. B. Franklin, K. A. Hamm, G. C. White, et al. 2021. "Invader Removal Triggers Competitive Release in a Threatened Avian Predator." *Proceedings of the National Academy of Sciences of the United States of America* 118(31): e2102859118. https://doi.org/10.1073/pnas.2102859118.

Wiens, J. D., K. M. Dugger, D. B. Lesmeister, K. E. Dilione, and D. C. Simon. 2020. "Effects of Barred Owl (*Strix varia*) Removal on Population Demography of Northern Spotted Owls (*Strix occidentalis caurina*) in Washington and Oregon—2019 Annual Report." U.S. Geological Survey Open-File Report 2020-1089.

Wilk, R. J., D. B. Lesmeister, and E. D. Forsman. 2018. "Nest Trees of Northern Spotted Owls (*Strix occidentalis caurina*) in Washington and Oregon, USA." *PLoS One* 13(5): e0197887. https://doi.org/10.1371/journal.pone.0197887.

Wood, C. M., H. Klinck, M. Gustafson, J. J. Keane, S. C. Sawyer, R. J. Gutiérrez, and M. Z. Peery. 2021. "Using the Ecological Significance of Animal Vocalizations to Improve Inference in Acoustic Monitoring Programs." *Conservation Biology* 35(1): 336–45. https://doi.org/10.1111/cobi.13516.

Wood, C. M., V. D. Popescu, H. Klinck, J. J. Keane, R. J. Gutiérrez, S. C. Sawyer, and M. Z. Peery. 2019. "Detecting Small Changes in Populations at Landscape Scales: A Bioacoustic Site-Occupancy Framework." *Ecological Indicators* 98: 492–507. https://doi.org/10.1016/j.ecolind.2018.11.018.

Wood, C. M., S. M. Schmidt, and M. Z. Peery. 2019. "Spatiotemporal Patterns of the California Spotted Owl's Territorial Vocalizations." *Western Birds* 50(4): 232–42. https://doi.org/10.21199/wb50.4.2.

Yackulic, C. B., L. L. Bailey, K. M. Dugger, R. J. Davis, A. B. Franklin, E. D. Forsman, S. H. Ackers, et al. 2019. "The Past and Future Roles of Competition and Habitat in the Range-Wide Occupancy Dynamics of Northern Spotted Owls." *Ecological Applications* 29(3): e01861. https://doi.org/10.1002/eap.1861.

Zhou, B., C. W. Xia, Z. R. Chen, and W. H. Deng. 2020. "Individual Identification of Male Ural Owls Based on Territorial Calls." *Journal of Raptor Research* 54(1): 57–65. https://doi.org/10.3356/0892-1016-54.1.57.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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